

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 3600, 19 pp., 13 figures, 1 table

December 12, 2007

## *Oculogryphus*, A Remarkable New Genus of Fireflies from Asia (Coleoptera: Lampyridae)

M.-L. JENG,<sup>1</sup> MICHAEL S. ENGEL,<sup>2</sup> AND P.-S. YANG<sup>3</sup>

### ABSTRACT

An unusual new lampyrid genus, *Oculogryphus* Jeng, Engel, and Yang, new genus, and its type species, *Oculogryphus fulvus* Jeng, new species, from Vietnam, is described and figured. The genus is characterized by its filiform antennae, large and ventrally approximate compound eyes that are deeply emarginate posteriorly, largely exposed head (i.e., not covered by the pronotum), eight abdominal ventrites, rectangular abdominal tergites, absence of photogenic organs, and symmetric aedeagal sheath and genitalia in the male (the female is presently unknown). The genus does not adequately fit into any subfamily as they are currently defined, highlighting the difficulties of the subfamilial and tribal classification presently in use. Though most likely allied to Ototretinae or Luciolinae, the systematic position of *Oculogryphus* cannot be determined as currently there is no comprehensive phylogeny of Lampyridae and related groups. The species may rely on photic cues for purposes of mating. A key to the genera of Lampyridae (sensu Crowson) occurring in Palearctic East Asia, Oriental, and Australian regions is provided. Some taxonomic problems of Ototretinae are commented upon.

### INTRODUCTION

The family Lampyridae, commonly known as lightning bugs, fireflies, or glow worms in English, is one of the beetle groups closely

associated with human beings. Bioluminescence is an attractive and useful feature of these beetles, though it is not unique to Lampyridae and not all lampyrid species glow or flash (McDermott, 1964; Lloyd, 1971).

<sup>1</sup> Division of Entomology, Natural History Museum, and Department of Ecology & Evolutionary Biology, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66049-2811 (kamakili@ku.edu).

<sup>2</sup> Division of Invertebrate Zoology, American Museum of Natural History; Division of Entomology (Paleoentomology), Natural History Museum, and Department of Ecology & Evolutionary Biology, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66049-2811 (msengel@ku.edu).

<sup>3</sup> Department of Entomology, National Taiwan University, #1, Sec. 4, Roosevelt Road, Taipei 106, Taiwan (psyang@ccms.ntu.edu.tw).

Glowing ability can also be found in several elateroid families such as Elateridae, Omalidae, Phengodidae, and Rhagophthalmidae (Lloyd, 1971, 1979; Crowson, 1981; Branham and Wenzel, 2003; Grimaldi and Engel, 2005). Confirmed bioluminescent display for the purpose of mating is known in Rhagophthalmidae and Lampyridae (Branham and Wenzel, 2003), and precise control over bioluminescence is unique to the latter (Trimmer et al., 2001). The brilliant and delicate bioluminescent behavior has made fireflies common subjects in cultural activities and works of art since early times, especially in Eastern Asian countries (Kanda, 1935; Harvey, 1957; Yamamoto, 1968; Konishi, 1997; Yang, 1998). Nowadays firefly-watching is a popular and seasonally routine activity for ecological tourism in several Asian countries (Othman and Othman, 1998; Chen, 1999, 2003; Ho et al., 2002; Nallakumar, 2003; Ohba, 2004). Fireflies are also good subjects for education, conservation, and ecological and biodiversity research (e.g., Furuta, 1991; Kobayashi, 1991; Murakami, 1991; Lloyd, 1997, 1998, 1999, 2000, 2001, 2003; Faust, 2004; Ohba, 2004). In a practical application, the firefly luciferase gene and the enzyme it codes for has been used as an indicator or probe in biological and medical sciences, thereby further highlighting the broad importance of lampyrids for human endeavors (Grimaldi and Engel, 2005).

Lampyridae are small to medium-sized beetles, usually not longer than 3 cm, though some larviform females can be as large as 8 cm in length. They are nearly globally distributed, particularly thriving and diverse in warm, humid environments (McDermott, 1964). The larvae are mostly terrestrial and active hunters or opportunistic scavengers feeding on living or dead small invertebrates and/or vertebrates (Lawrence and Britton, 1994; Lloyd, 2002; Ho and Chu, 2002; Chen, 2003). Some unusual habitats including an intertidal spray zone, ant nests, marshes, running water, seepage environments, hot springs, and decaying tree trunks have also been reported (Annadale, 1900, 1906; Blair, 1927; Imms, 1933; Ballantyne and Buck, 1979; Buschman, 1984; Ohba and Goto, 1991; Sivinski et al., 1998; Lloyd, 2002; Jeng et al.,

2002, 2003b; Fu et al., 2005a). About 2000 species have been described (Nakane, 1991), and a considerable portion of them are active in the daytime (McDermott, 1964; Lloyd, 2002; Branham and Wenzel, 2003). Though attractive, diverse, and useful, Lampyridae did not have a clear definition until recently. Their family-group compositions and boundaries were altered frequently and dramatically during the past century. The modern classification of Lampyridae was fundamentally built on the basis of Olivier (1907, 1910), then modified and improved by Green (1948, 1959), Crowson (1955, 1972), McDermott (1964, 1966), Wittmer (1979), Nakane (1991), Lawrence and Newton (1995), Jeng et al. (1998a, 2006a, 2006b), Lawrence et al. (1999), and Branham and Wenzel (2001). Olivier (1907) published the first lampyrid catalogue in which he constructed a nine-subfamily system, largely based on antennal and head morphology. McDermott's seven-subfamily system (1964, 1966) reduced several of Olivier's subfamilies to subordinate units of Lampyrinae and added Matheteinae, Rhagophthalminae, and Pterotinae. Otoretinae was first treated as a subfamily in McDermott (1964) but later demoted to a lucioline tribe in McDermott (1966). McDermott (1964) also provided the latest comprehensive accounts on the family-group definitions and compositions. Crowson (1972) clarified the separation of Lampyridae from the other cantharoid families. He removed Rhagophthalminae to Phengodidae and Matheteinae to Omethidae, transferred many genera of Drilidae to Otoretinae, and established Cyphonocerinae and Otoretadrilinae based on former drilid genera. Crowson did not address much on the content of each subfamily but gave a tentative key to the eight lampyrid subfamilies he suggested. In total, 23 family-group taxa based on different type genera have been proposed across the three major classifications (Olivier, 1907; McDermott, 1964; Crowson, 1972) (table 1). The classification of Lampyridae currently used is essentially a mix of McDermott's and Crowson's systems: adopting Crowson's eight-subfamily system and following McDermott's generic composition of each subfamily (e.g., Lawrence and Newton, 1995; Lawrence et al.,

TABLE 1  
Modern Family-group Classifications of Lampyridae

Olivier, 1907 (9 subfamilies, 48 genera)	McDermott, 1966 (7 subfamilies, 85 genera)	Crowson, 1972 <sup>a</sup> (8 subfamilies)
Subfamily Lampyrinae Latreille (9) <sup>b</sup>	Subfamily Lampyrinae Latreille (53)	Subfamily Lampyrinae Latreille
Subfamily Lamprocerinae Olivier (14)	Tribe Lampyrini Latreille (11)	Subfamily Amydetinae Olivier
Subfamily Photininae LeConte (6) <sup>c</sup>	Tribe Pleotomini Green (5)	Subfamily Photurinae Lacordaire
Subfamily Lucidotinae LeConte (7)	Tribe Lamprocerini Olivier (5)	Subfamily Luciolinae Lacordaire
Subfamily Dadophorinae Olivier (1)	Tribe Cratomorphini Green (5)	Subfamily Ototretinae McDermott
Subfamily Megalophthalminae Olivier (2)	Tribe Photinini LeConte (27)	Subfamily Pterotinae LeConte
Subfamily Amydetinae Olivier (1)	Subtribe Photinina LeConte (13)	Subfamily Cyphonocerinae Crowson
Subfamily Photurinae Lacordaire (1)	Subtribe Lucidotina Lacordaire (10)	Subfamily Ototretadrilinae Crowson
Subfamily Luciolinae Lacordaire (7)	Subtribe Dadophorina Olivier (1)	
	Subtribe Phosphacina McDermott (2)	
	Subtribe Lamprigerina McDermott (1)	
	Subfamily Amydetinae Olivier (12)	
	Tribe Amydetini Olivier (2)	
	Tribe Vestini McDermott (5)	
	Tribe Psilocladini McDermott (5)	
	Subfamily Photurinae Lacordaire (4)	
	Subfamily Luciolinae Lacordaire (9)	
	Tribe Luciolini Lacordaire (6)	
	Tribe Curtosini McDermott (1)	
	Tribe Ototretini McDermott (2)	
	Subfamily Matheteinae LeConte (2)	
	Subfamily Pterotinae LeConte (1)	
	Subfamily Rhagophthalminae Olivier (4)	

<sup>a</sup> The more recent classifications of Nakane (1991) and Branham and Wenzel (2001) recognized the same eight subfamilies although with modified generic compositions for Lampyrinae, Amydetinae, and Cyphonocerinae (the synonymy of Cyphonocerinae by Jeng et al. [1998a] was based on Nakane's [1991] redefinition of the subfamily). Branham and Wenzel's cladistic study indicated that Lampyrinae, Amydetinae, and Ototretinae were polyphyletic; that Luciolinae and perhaps Photurinae were monophyletic; that Ototretinae and Pterotinae should be considered incertae sedis in Elateroidea; while the status of two subfamilies could not be commented upon (Ototretadrilinae was excluded and Cyphonocerinae was represented by a single genus). Kazantsev (2006) created Cheguevarini and tentatively placed the tribe as incertae sedis in Lampyridae.

<sup>b</sup> Value in parentheses indicates the number of explicitly included genera.

<sup>c</sup> A name homonymous with the subfamilial name Photininae Giglio-Tosi, in the Mantidae (Mantodea).

1999), or with some minor modifications (e.g., Wittmer, 1979; Nakane, 1991; Jeng et al., 1998a). However, Branham and Wenzel's (2001) phylogenetic analysis revealed that all of the subfamilies currently recognized, except Luciolinae and perhaps Photurinae, are paraphyletic or polyphyletic, or not lampyrids at all. The definitions of Lampyridae and their subordinate units will need a comprehensive revision (underway by the senior author).

Recently we identified a remarkable new genus of Lampyridae from Vietnam. Its unique combination of characters does not fit the definition of any subfamily or tribe/subtribe currently recognized, further highlighting the difficulties of the present higher

classification of the family. Herein we provide a description of this enigmatic new group, making its name available for forthcoming contributions to the familial classification, to alert coleopterists to its presence and discuss its systematic position among other fireflies.

## MATERIAL AND METHODS

The material was from the late Dr. M. Satô's personal collection. The glued specimen was first softened and released in hot water and then preserved in 80% ethanol solution for dissection and illustration. Male genital segments were dissected and soaked in 10% potassium hydroxide (KOH) solution at room

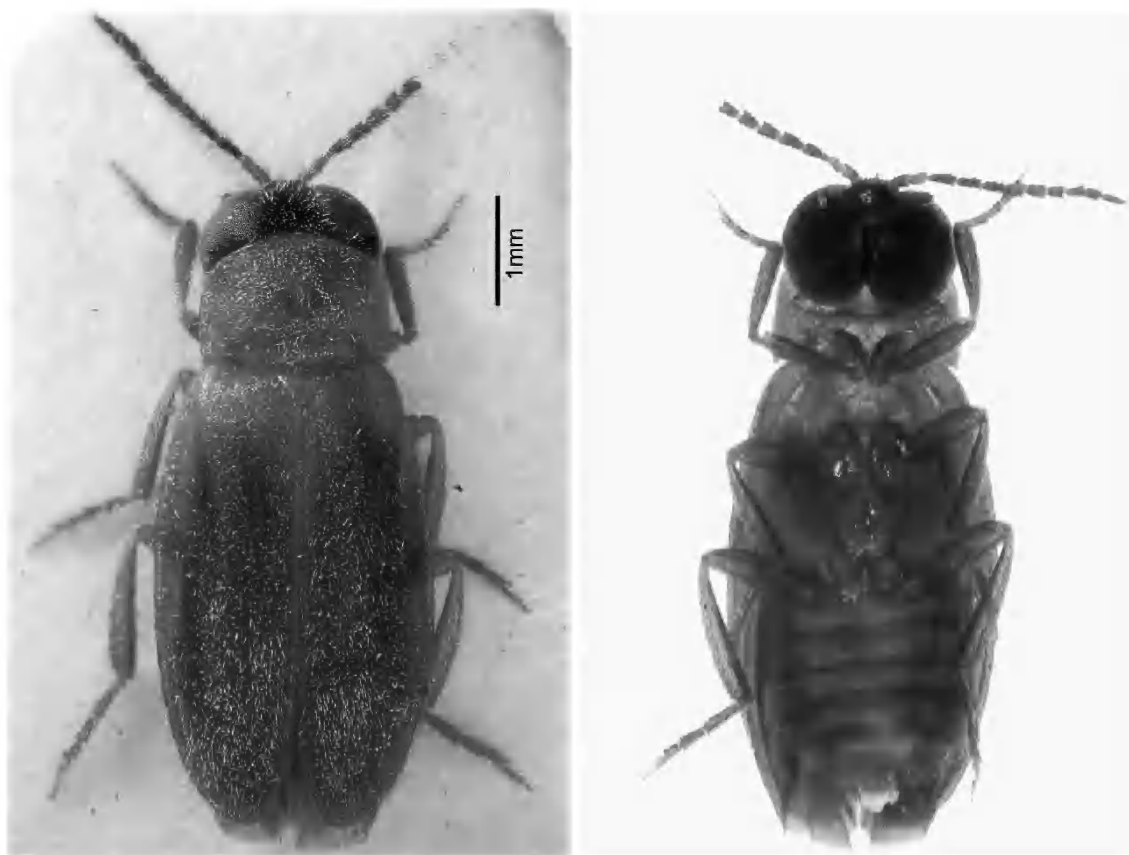


Fig. 1. Habitus of holotype male of *Oculogryphus fulvus*, new genus and species, dorsal (left) and ventral (right) aspect.

temperature for 24 hours prior to examination. The abbreviations BL, BW, EL, EW, PL, and PW are employed for “body length”, “body width”, “elytral length”, “elytral width”, “pronotal length”, and “pronotal width”, respectively. Body length is the distance between the anterior head margin and elytral apex; body width is the greatest distance across the elytra or twice the width of an elytron ( $BW = 2EW$ ). The term “ventrite” is used for the visible abdominal sternite; T# and S# replace the true #th tergite or sternite of the abdomen, respectively; the last abdominal tergite is T8; “aedeagal sheath” is composed of a syntergite (T9 + 10) and sternite IX [S9 = ventrite 8 (V8)]. It should be noted that Ballantyne and Lambkin (2001, 2006) used ventrite to reflect the sternite of true segmentation (e.g., V8 = S8). We have followed the typical method of using

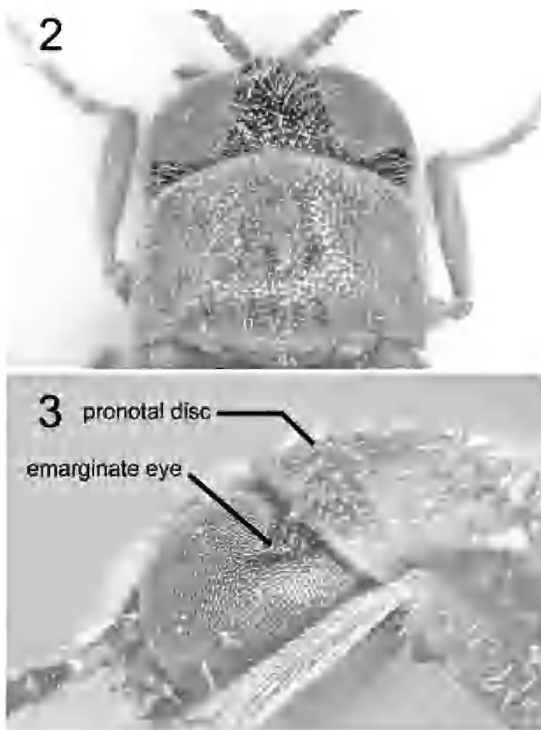
“ventrite” for the purpose of visual diagnosis without difficulty, and “sternite” for the identification of morphological homologues across taxa. The nomenclature of hind-wing venation follows that of Kukalová-Peck and Lawrence (1993).

## SYSTEMATICS

### *Oculogryphus* Jeng, Engel, and Yang, new genus

TYPE SPECIES: *Oculogryphus fulvus* Jeng, new species (fig. 1).

DIAGNOSIS: The new genus can be readily diagnosed by the following combination of characters: partially exposed head; 11-articled, filiform antennae; large compound eyes that are emarginate posteriorly and approximate ventrally; strongly curved and crossing man-



Figs. 2–3. *Oculogryphus fulvus*, new genus and species, male, head and pronotum. 2. Dorsal aspect. 3. Lateral aspect.

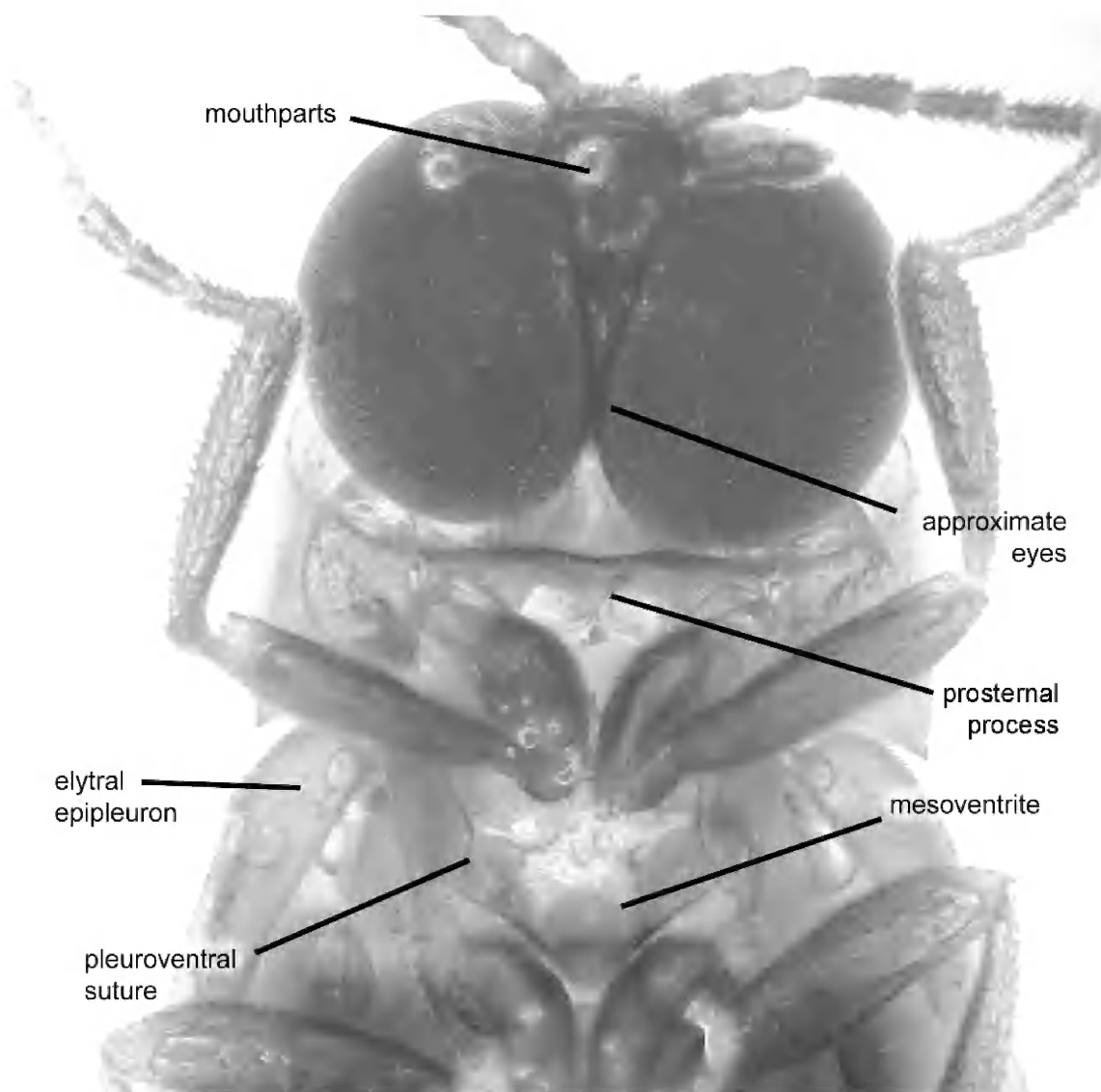
dibles with pointed apex; narrowly explanate pronotal margins and close pronotal hypomeron; epipleuron restricted to basal half of elytra; eight abdominal ventrites (including exposed sternite of aedeagal sheath); abdominal tergites not lobed; absence of photogenic organs and tibial spurs; and progressively shortened tarsomeres 1–4. These characters intermingle diagnostic features of Luciolinae, Rhagophthalmiinae, and Otoretinae, but none of the three subfamilies possess all of these characters.

**DESCRIPTION: Male.** Body shape elongate oval, somewhat depressed and fully winged. Head (fig. 2) largely exposed from pronotum when retracted, intermediate between prognathous and hypognathous. Compound eyes very large, occupying most of head laterally and with hind margins remarkably emarginate (fig. 3); compound eyes separated from each other in dorsal aspect by about one-third head width and approximate ventrally (fig. 4). Vertex flat or slightly depressed. Antennal calli (convexity above antennal sockets: see

DuPorte, 1960) weakly convex; antennal socket elongate elliptical in shape, moderately distant from labrum, with antennifer in lower margin of socket; space between antennal sockets slightly convex, about as broad as one-half width of socket; antennae 11-articled, filiform, reaching elytral base when in repose; scape and pedicel elongate, longer in former; flagellar articles cylindrical and densely setose. Lower margin of clypeus broadly and roundly emarginate. Labrum sclerotized, notched medioapically. Mandibles well developed, strong and nearly uniform in diameter to near tip, curved and pointed apically. Maxillae with cardines approximate each other at base; maxillary palpi with four palpomeres, labial palpi with three palpomeres, both with slightly dilated, thick, terminal palpomeres and bud-like apices, without thin ridge or tooth on inner side. Ventral margin of occipital foramen emarginate, reaching basal one-third of head length. Gula very narrow. Posterior tentorial pits immediately behind labrum, at about middle of head. Margins of hypostoma convergent toward base (fig. 4).

Pronotum (fig. 2) transverse, subparallel-sided, punctate, and pubescent throughout; mostly opaque although translucent on margins; anterior margin broadly rounded, without clear anterolateral angles; central disc evenly convex (fig. 3), with median sulcus; apical and lateral explanate margins very narrow; posterolateral angles large and nearly orthogonal; posterior margin weakly sinuate, broadly impressed on inner base of posterior angles. Hypomeron close in frontal aspect, with inner margin attending anterolateral margin of pronotum. Prosternum (fig. 4) with an inverted Y-shaped, short and broad intercoxal process. Mesoventrite separated from mesopleurites by a clear suture (fig. 4). Metaventrite notched medioapically. Elytra elongate oval, well paired along midline; carinae weak; lateral explanate margins narrow; surface covered with fine setae. Humeral area of elytra (fig. 5) roundly folded toward marginal costa; epipleura narrow, deeply folded, barely visible laterally, extending from humeral base to basal one-third of elytra. Venation of hind wing (fig. 8) with reduction of crossveins; radial cell incomplete;  $MP_{3+4}$  and  $CuA_{1+2}$  not connected by crossveins and





Figs. 4. *Oculogryphus fulvus*, new genus and species, male, head and thorax, ventral aspect.

not branched. Legs long and slender. Front trochantins setiferous but glabrous in middle legs. Mesocoxae moderately separated from each other; metacoxae narrowly separated from each other. Tibial spurs absent. Tarsi (fig. 9) about as long as their tibiae in middle and hind legs; tarsomeres progressively shorter from 1–4, cylindrical and slender in 1–3; tarsomere 4 with tarsal pulvillus and lobed, widely open in dorsal cleft (fig. 9); pretarsal claws simple.

Abdomen with eight ventrites (fig. 11, S2–9), reaching elytral apices. Spiracles in lateral folded, membranous pleurites, not visible ventrally. Tergites invisible in ventral aspect, not lobed and with rounded posterior angles. Apical margin of ventrite 7 (= S8) simple; exposed portion of V8 (= S9) semirounded. Aedeagal sheath basically symmetric, broad and short; T9 and T10 individually distinct; S9 broad at base. Male genitalia modified trilobed, bilaterally symmetric; much smaller

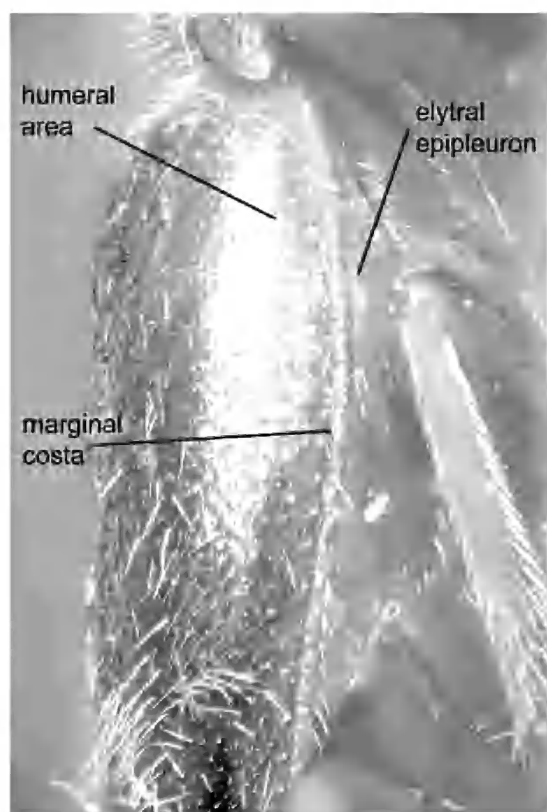


Fig. 5. *Oculogryphus fulvus*, new genus and species, male, basal half of elytra, lateral aspect.

than aedeagal sheath; median lobe uniformly broad, arched upward in apical half; parameres broad in lateral aspect and forming a V-shaped band in dorsal aspect; basal piece large and symmetric.

**Female.** Unknown.

**ECOLOGY:** Unknown; see Discussion, below.

**ETYMOLOGY:** The new genus-group name is a combination of the Latin terms *oculus* (meaning "eye") and *gryphus* (meaning "griffin", originally a mythological creature from Asia adopted by the Greeks and with a mix of features from a lion and an eagle. The idea of the griffin perhaps stemmed from ancient people's seeing the exposed remains of *Protoceratops*: Mayor, 2000). The name is a reference to the characteristic eyes and the ambiguous, subfamilial identity of the new genus. The name is masculine.

**DIVERSITY:** The type species is presently the only known member of the genus.

*Oculogryphus fulvus* Jeng, new species  
Figures 1–13

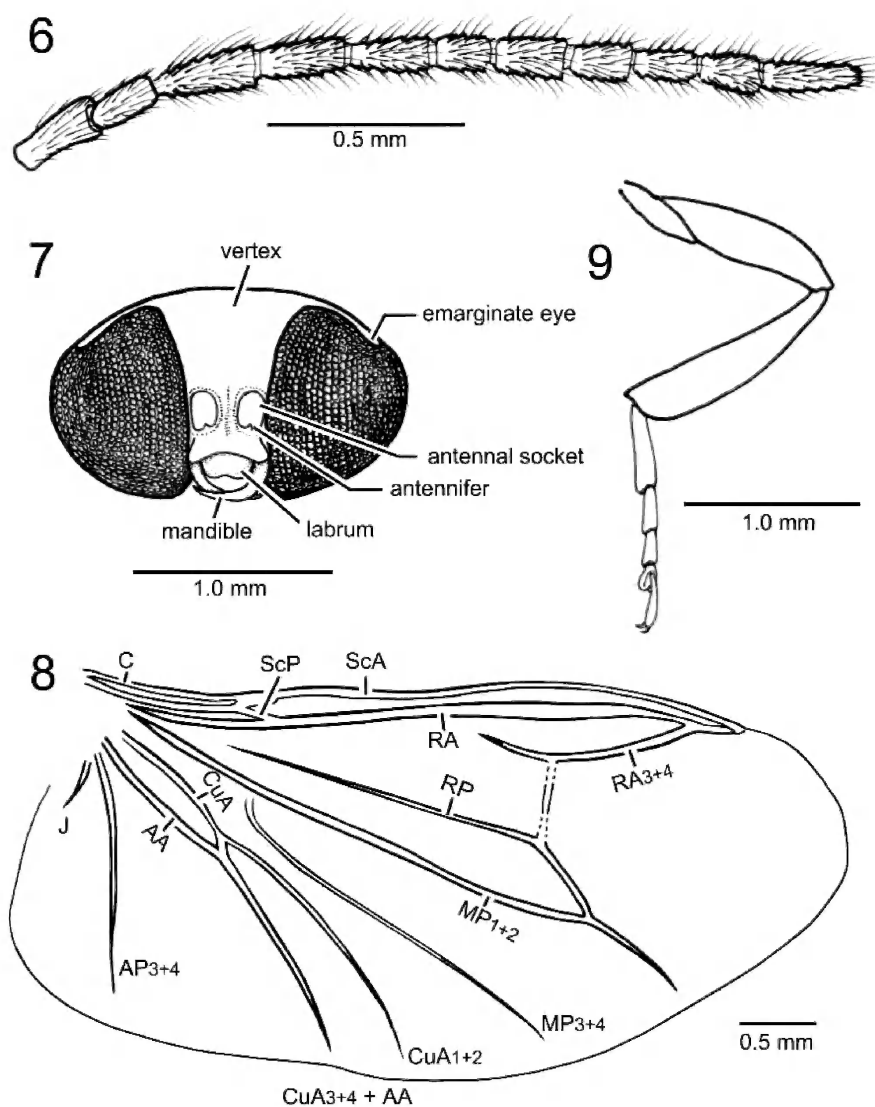
**TYPE LOCALITY:** Tam Dao, Province Vinh Phu, Vietnam.

**DIAGNOSIS:** As for the genus (see above).

**DESCRIPTION:** **Male.** BL 6.0 mm, BW 2.5 mm; body form elongate oval and somewhat depressed; overall coloration brown except vertex black; antennal scape and pedicel brown, flagellar articles dark brown; elytra brown, looking darker from basal fifth to apices due to shadows of hind wings; venter brown throughout. Head with vertex and beyond exposed from above, not hidden by pronotum; vertex flat between eyes, surface glabrous, densely punctate and pubescent. Distance between compound eyes about two-fifths of greatest width of head in dorsal aspect, one-fifth in frontal aspect (fig. 7), and one-sixth in ventral aspect. Antennae (fig. 6) with scape elongate quadrate in dorsal aspect, about as long as first flagellar article (FA1); FA1–3 each subequal in length, 4–8 each subequal in length and shorter than 1–3; FA 9 (terminal antennomere) spindle-like.

Pronotum subparallel-sided; posterior angles sharply cornered; punctures on disc separated by about their own diameter (fig. 2). Scutellum large and triangular in shape. Elytra with well-defined lateral margins; surface more or less shagreened, densely setose, costae insignificant except sutural costae. Elytral epipleuron (fig. 5) deeply folded, lying in ventral side of elytra and nearly invisible from lateral aspect, about one-sixth of elytral length. Mesoventrite (fig. 4) broadly V-shaped. Central longitudinal sulcus of metaventrite obsolete. Abdominal T8 (fig. 10) broadly rounded apically and slightly emarginate medioapically, S8 (fig. 11) subtrapezoidal. PW/PL = 1.4; EL/EW = 3.3; EL/PL = 3.4; BW/PW = 1.5.

Aedeagal sheath (fig. 12) about 0.7 mm long, 0.4 mm broad; syntergite slightly surpassing apex of S9; T9 about as long as T10; T10 triangular; S9 setose in apical one-third, rounded at apex, tapering toward base. Genitalia (fig. 13) about 0.5 mm long, 0.3 mm broad; median lobe parallel sided in basal half and gradually tapering apically in dorsal aspect; paramere weakly sclerotized apically but strongly so in posterior margin; dorsum



Figs. 6–9. *Oculogryphus fulvus*, new genus and species, male. **6.** Antenna. **7.** Head, frontal aspect; antennae and most of the mouthparts except mandibles and labrum were not shown. **8.** Hind wing. **9.** Hind leg, trochanter to tarsus.

forming a widely V-shaped band connecting with median lobe; basal piece about as long as median lobe, bilaterally symmetric, roughly a V-shaped band, slightly pointed apically.

**Female.** Unknown.

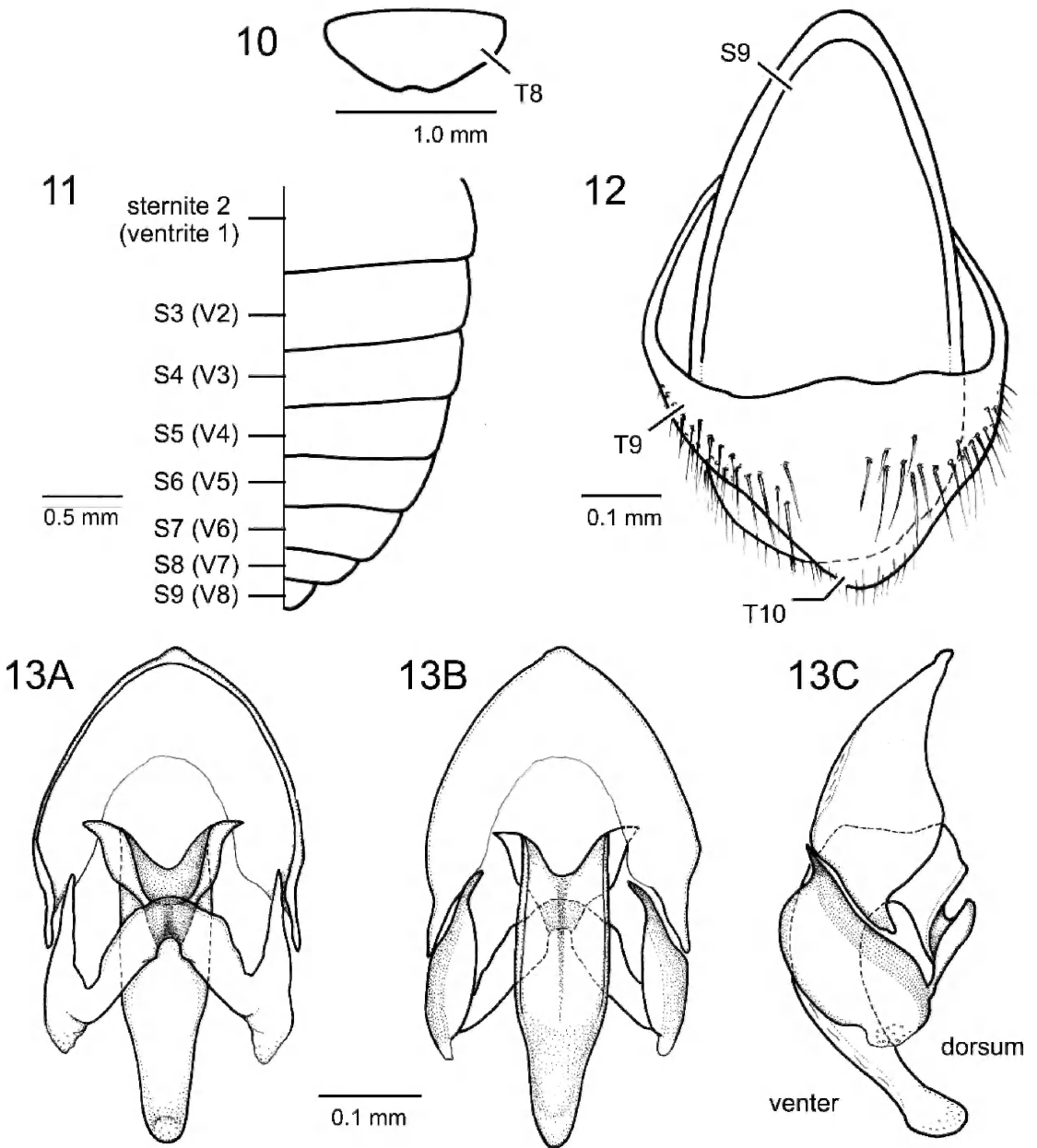
**TYPE MATERIAL:** Holotype, male; “N. Vietnam 1985, pr. Vinh phu, Tam dao 3.6.-11.6. V. Švihis lgt.”. The holotype will be preserved in the National Museum of Natural Science, Taichung City, Taiwan (NMNS).

**ETYMOLOGY:** The specific epithet refers to the light brown coloration of the species.

**KEY TO LAMPYRID GENERA IN EAST AND SOUTHEAST ASIA AND AUSTRALIA**  
(males only)

The considered area ranges from India in the west and Australia in the east, zoogeographically including the whole Oriental region





Figs. 10–13. *Oculogryphus fulvus*, new genus and species, male. **10.** Abdominal tergite 8, dorsal aspect. **11.** Abdominal visible sternites, right half, ventral aspect. **12.** Aedeagal sheath, dorsal aspect. **13.** Male genitalia, dorsal (A), ventral (B), and lateral (C) aspects.

(OR, including Indian subcontinent, Himalayas, Indochina and Malay Peninsula, Taiwan, Philippines, Borneo, and Sunda Islands), the Palaearctic region in East Asia (PA, including Eastern Eurasia continent, Korean Peninsula, and Japan-

Ryukyu Archipelago), New Guinea, Pacific islands, and Australia of the Australian region (AU). The proposed key, following Crowson's definition of Lampyridae, provides an account of the 34 lampyrid genera presently documented in this area (inclusive

of the new genus). It is partly based on or modified from Ballantyne and Lambkin (2001, 2006, for couplets 3–10), Maulik (1921) and Wittmer (1979) (for couplets 22–24), and Wittmer (1937, for couplet 33). It should be noted that the key is tentatively proposed, especially for the nontypical lampyrids (couplet 20 and below). With the exception of *Oculogryphus*, most of the nontypical lampyrid genera were transferred from Drilidae and placed under Ototretinae or Ototretadrilinae by various authors. Most of them are poorly known at present, usually with no more than revisional works on restricted zoogeographic faunas (e.g., *Drilaster* of Ryukyu Archipelago by Kawashima et al., 2005). Characters for these genera are provided herein based on examination of the type species (\*), together with some additional exemplar species (\*\*), on some nontype species only (#), or in a few cases on references alone (§).

1. Abdomen with six visible sternites (ventrites) 2
  - Abdomen with more than six ventrites . . . 12
2. Antennae serrate and depressed; coloration of elytra pink to various degrees . . . . .
  - . . . . . *Pristolytus* Gorham (OR, PA)
  - Antennae filiform or somewhat moniliform; coloration of elytra never pink . . . . . 3
3. Compound eyes with posterior margin clearly emarginate<sup>4</sup> . . . . . *Bourgeoisia* Olivier (OR) and *Luciola cowleyi* Blackburn (AU)
  - Compound eyes never or insignificantly emarginate posteriorly . . . . . 4
4. Elytron with superimposed costa arising from humeral area and extending to near apex . . . . . *Curtos* Motschulsky (OR, PA)
  - Elytron without clear humeral costa; if present, not particularly more imposed than other costae . . . . . 5
5. Median apical area of abdominal tergite 8 narrowed and deflexed, closely approaching the incurved and hooked apex of ventrite 6; some species with acute and conspicuous anterior angles on pronotum . . . . .
  - . . . . . *Pygoluciola* Wittmer (OR)
  - Median apical area of abdominal tergite 8 not narrowed or deflexed; anterior angles of pronotum never acute . . . . . 6
6. Apices of parameres of genitalia largely or totally concealed by median lobe, not visible in ventral aspect . . . . . 7
  - Apices of parameres of genitalia barely or not concealed by median lobe, visible in ventral aspect . . . . . 10
7. Apex of elytra deflexed . . . . .
  - . . . . . *Pteroptyx* Olivier (OR, AU)
  - Apex of elytra not deflexed . . . . . 8
8. Median carina of V6 present . . . . .
  - . . . . . *Colophotia* Dejean (OR)
  - Median carina of V6 absent . . . . . 9
9. Photogenic organs on V6 bipartite; aedeagal sheath bearing paraprocts . . . . .
  - . . . . . *Pyrophanes* Olivier (OR, AU)
  - Photogenic organs on V6 one-pieced; aedeagal sheath without paraprocts . . . . .
    - . . . . . some *Luciola* species<sup>5</sup> (PA, OR, AU)
10. Elytra broad, with lateral explanate margin of elytra quite broad in elytral base, unambiguously visible in humeral area dorsally; usually at least two elytral costae well developed; hypomeron with frontal margin at angle of 30–45 degrees with pronotal lateral margin laterally . . . . . 11
  - Elytra more or less elongate, with lateral explanate margin of elytra very narrow in humeral basal area, thus partially concealed by humerus dorsally; elytral costae usually poorly developed, or weakly developed; hypomeron with frontal margin at angle of 70–90 degrees with pronotal lateral margin laterally . . . *Luciola* Laporte de Castelnau (OR, PA, AU) and *Hotaria* Yuasa<sup>6</sup> (PA)
11. Abdominal tergite 8 asymmetric bilaterally . .
  - . . . . . *Luciola ovalis* group (OR)
  - Abdominal tergite 8 symmetric bilaterally . .
    - . . . . . *Atyphella* (including s.g. *Pygatyphella*, AU)
12. Antennae bipectinate . . . . .
  - . . . . . *Cyphonocerus* Kiesenwetter (PA, OR)
  - Antennae not bipectinate . . . . . 13

<sup>5</sup> Including *Luciola flavicollis* Macleay, *L. orapallida* Ballantyne, and *L. nigra* Olivier from Australia, *L. kuroiwae* Matsumura from Ryukyu, *L. trilucida* from Taiwan, and some undetermined species from Indochina Peninsula.

<sup>6</sup> *Hotaria* was treated as a subgenus by McDermott (1966), or a synonym of *Luciola* by Kawashima et al. (2003). Indeed, *Hotaria* and *Luciola* s.str. (based on *L. italica*) shared many morphological characters in males as well as flightless females which have complete elytra but absence of hind wings. Ballantyne and Lambkin's (2001, 2006) phylogenetic analyses suggest a close relationship of these two groups. However *Luciola* currently recognized is a highly diverse group, containing more than 300 species worldwide, and definitely needs a redefinition. Accordingly we have kept *Hotaria* as a valid name until its status is decided phylogenetically.

<sup>4</sup> Some species of *Lampyroidea* have compound eyes with an emarginate posterior margin in males, but the genus does not occur in the area and is therefore excluded from the key.

13. Head fully covered by pronotum in dorsal aspect when fully retracted . . . . . 14
  - Head largely or partially exposed from pronotum when fully retracted, eyes always visible at least partially in dorsal aspect . . . . . 19
14. Spiracles at or approximate to lateral edges of ventrites, visible in ventral aspect . . . . . 15
  - Spiracles on dorsally folded part of ventrites, not visible in ventral aspect . . . . . 17
15. Tibial spurs present; abdominal photogenic organs vestigial, represented by small spots, while compound eyes large and separated from each other by less than compound-eye width in ventral aspect . . . . .
  - . . . . . *Lampyrus* Geoffroy (PA, OR)
  - Tibial spurs absent; photogenic organs usually well developed as transverse stripes, if reduced and spotlike, then accompanied with small and widely separated compound eyes . . . . . 16
16. Compound eyes moderate in size, separated from each other by distance of about an eye width in ventral aspect; pronotum flat or slightly convex in apical one-third to half length of pronotum, with central disc occupying basal three-fifths to two-thirds of pronotal length; antennae never filiform; photogenic organs reduced in diurnal species . . . . . *Pyrocoelia* Gorham (OR, PA)
  - Compound eyes large in size, approximate ventrally; pronotum distinctly convex in apical half to two-thirds of pronotal length, forming a light bulb-like convexity together with pronotal central disc which as long as or shorter than convex area; antennae serrate, filiform, or pectinate; photogenic organs well developed *Diaphanes* Motschulsky (OR, PA)
17. Compound eyes large and deeply emarginate in posterior margin, approximate each other ventrally; antennae short, with small projected sensory appendages on several terminal flagellar articles; pronotal pleurite subtriangular, about as long as height . . . . .
  - . . . . . *Lamprigera* Motschulsky (OR, PA)
  - Compound eyes small and not deeply emarginate in posterior margin, widely separated ventrally; antennae long, serrate, compressed or pectinate, without those small appendages as above; pronotal pleurite subtrapezoid, longer than height . . . . . 18
18. Male genitalia with a pair of slender appendages originating from apical region of parameres; parameres not forming a basal projection in dorsal aspect; pretarsal claws simple on all legs . . . . .
  - . . . . . *Vesta* Laporte de Castelnau (OR, PA)
  - Male genitalia with a pair of lateral appendages along median lobe; parameres forming a basal projection in dorsal aspect; pretarsal claws of fore- and midlegs each with a ventral projection on one claw (in many species) . . . . . *Lucidina* Gorham<sup>7</sup> (OR, PA)
19. Elytra dehiscent, not fully covering abdomen . . . . . 20
  - Elytra well matching along central suture, fully covering abdomen or nearly so . . . . . 21
20. Antennae somewhat pectinate; terminal antennal article not reduced . . . . .
  - . . . . . *Ototretadrilus* Pic<sup>#</sup> (OR)
  - Antennae not pectinate, more or less depressed; terminal antennal article reduced . . . . . *Baolacus* Pic<sup>§</sup> (OR)
21. Both maxillary and labial palps greatly lobed, much wider than antennae . . . . . 22
  - Both maxillary and labial palps of normal size, not wider than antennae . . . . . 25
22. Antennae unipectinate . . . . . 23
  - Antennae weakly serrate or filiform . . . . . 24
23. Antennomeres 3–10 very long and narrow, almost cylindrical; antennal branches not much longer than their stem antennomeres . . . . . *Eugeusis* Westwood\* (OR)
  - Antennomeres 3–10 short and broad, flat; antennal branches about 3–4 times length of their stem antennomeres . . . . . *Hyperstoma* Wittmer<sup>§</sup> (OR)
24. Compound eye less than one-quarter of head width in dorsal aspect; genae behind compound eyes (temple) exposed; antennae widely separated from each other . . . . .
  - . . . . . *Lamellipalpus* Maulik\*\* (OR)
  - Compound eye about of one-quarter head width; temple covered by pronotum; antennae more or less approximate . . . . . *Lampellipalpodes* Maulik\* (OR)
25. True abdominal sternite 2 long, weakly sclerotized in anterior part but uniformly sclerotized on central disc, largely exposed in ventral aspect as first ventrite, with its posterior margin reaching base of metatrochanters; abdominal spiracles at edge of pleural membrane and dorsally folded portion of sternites, scarcely visible directly in dorsal aspect when elytra and hind wings removed . . . . . 26
  - True abdominal sternite 2 short, weakly sclerotized centrally, largely concealed by metatrochanters and barely visible in ventral aspect, with its posterior margin usually not

<sup>7</sup> *Lucidotopsis* McDermott is essentially a synonym of *Lucidina* s.str. and will be discussed in a forthcoming paper. The monotypic genus *Mimophotinus* Pic, based on *M. angustatus* Pic from Vietnam, was also allied to nontypical *Lucidina*. Their relationship will need further investigation.

- reaching base of metatrochanters; abdominal spiracles entirely enclosed by dorsally folded portion of sternites, always visible in dorsal aspect when elytra and hind wings removed . . . . . 29
26. Antennae serrate; tibial spurs present . . . . . *Falsophaeopterus* Pic\*\* (OR)
- Antennae unipectinate or filiform; tibial spur absent. . . . . 27
27. Antennae filiform; compound eyes with posterior margin significantly emarginate . . . . . *Oculogryphus*, n. gen.\* (OR)
- Antennae unipectinate; compound eyes not emarginate on posterior margin . . . . . 28
28. Pronotum with posterior margin round, surpassing posterolateral angles. . . . .
- . . . . . *Harmatelia* Gorham\* (OR)
- Pronotum with posterior margin straight, not surpassing posterolateral angles . . . . .
- . . . . . *Stenocladus* Fairmaire\*\* (PA, OR)
29. Posterior margin of pronotum round, surpassing posterolateral angles. . . . . 30
- Posterior margin of pronotum nearly straight, not surpassing posterolateral angles. . . . . 31
30. Antennae weakly serrate or somewhat filiform, with flagellar articles symmetric on lateral sides; first tarsomere of hind leg slightly longer than following article. . . . .
- . . . . . *Ceylanidrilus* Pic\*\* (OR)
- Antennae strongly serrate, with flagellar articles asymmetric on lateral sides; first tarsomere of hind legs 1.5 times longer than following article. . . . .
- . . . . . *Gorhamia* Pic\* (OR), *Pachytarsus* Motschulsky<sup>#</sup> (OR)
31. Antennae pectinate. . . . . *Flabellotreta* Pic\*\* (OR)
- Antennae not pectinate. . . . . 32
32. Antennae about as long as body, strongly serrate, with flagellar articles elongate triangular, clearly asymmetric on lateral sides. . . . . *Mimophaeopterus* Pic\*\* (OR)
- Antennae not as long as body, more or less filiform, with flagellar articles weakly serrate, symmetric, or slightly asymmetric on lateral sides. . . . . 33
33. Pedicel of antenna about twice as long as wide; antennal sockets weakly convex above. . . . .
- . . . . . *Drilaster* Kiesenwetter\*\* (OR, PA)
- Pedicel of antenna abbreviated, about as long as broad; antennal sockets convex above . . . . .
- . . . . . *Picodrilus* Wittmer\* (OR)

## DISCUSSION

Although no behavioral data are available for *Oculogryphus fulvus*, its morphology provides some possible clues into the biology of

this remarkable beetle. *Oculogryphus* has filiform antenna, large and ventrally approximate compound eyes but lacks photogenic organs in males. It is likely that the males primarily rely on bioluminescent cues emitted by females to find their mates at night or during twilight hours. Similar male morphology can be found in genera like *Lampyrus* Geoffroy, *Nyctophila* Olivier, *Rhagophthalmus* Motschulsky, among others. Lloyd (1971) termed this kind of intersexual communication as Type I<sup>8</sup>. Usually the females of this type are flightless and sedentary on the ground.

The new genus will arguably key to Rhagophthalminae, Luciolinae, or Otoretinae by using McDermott's (1964) or Crowson's (1972) key. Actually, neither of the keys satisfies the morphological combination of *Oculogryphus*. Many of its characters agree with the three subfamilies. For example, the partially exposed head; short pronotum; narrow pronotal margins, close hypomerion, roundly folded humeral area, narrow elytral epipleuron; broadly V-shaped mesoventrite; slender and long legs; nonlobed abdominal tergites narrower than ventrites; and many other traits are all suggestive of these subfamilies. However, most of these shared similarities appear to be sympleisomorphic from a simple outgroup comparison. There are few but remarkable differences between *Oculogryphus* and Rhagophthalminae/Luciolinae/Otoretinae. These are the antennal morphology, the number of abdominal ventrites, presence/absence of photogenic organs, compound eye morphology, and abdominal structures (discussed in detail in the following paragraphs below).

Rhagophthalminae are a controversial family-group taxon among elateroids. The subfamily was established by Olivier (1907) under Lampyridae, then became an independent family three years later (Olivier, 1910). Crowson (1955) placed it back as a lampyrid subfamily and this classification was adopted by McDermott (1964, 1966). Less than a decade later, Crowson (1972) transferred the genera of Rhagophthalminae to Phengodidae but did not specify whether Rhagophthalminae were still a valid group therein. Lawrence and Newton

<sup>8</sup> Type II includes those species with interactive photic communications between the sexes.

(1995) listed Rhagophthalminae as an Old World lineage of Phengodidae. Suzuki (1997) suggested that *Rhagophthalmus* had a close relationship with some genera of Otoretinae, whereas Lawrence et al. (1999) revived the familial status of Rhagophthalmidae. McDermott and Wenzel (2001, 2003) demonstrated a distant relationship of Rhagophthalminae and Phengodidae, and the former was tied with Lampyridae and other cantharoids in a trichotomy. Its position in Elateroidea is still highly debatable.

McDermott's (1964) key differentiated Rhagophthalminae from the other lampyrid subfamilies by the largely exposed head of the former. This is only partially true for a few genera like *Diophtoma* Pascoe, *Ochotyra* Pascoe, and some species of *Rhagophthalmus*. These genera have their pronotum slightly narrower than the head so that the head is not retractable into the prothoracic collar. We examined nine out of the 12 known rhagophthalmine genera along with an undetermined genus and found that most of the other rhagophthalmine genera have their heads partially covered by the pronotum, as in Luciolineae and Otoretinae. Our observations also reveal that all genera but *Diophtoma* have a telescope-like abdominal segment 9 + 10 and 12-articled antennae in males. Among the other cantharoids only some phengodid genera possess a combination of these two derived characters. In addition, the larviform females and larvae of these two family-group taxa resemble each other considerably. It is, therefore, hardly a surprise why some coleopterists suggested their affinity. However, Phengodidae themselves are highly diverse. The tribes Mastinocerini and Penicillophorini deviate greatly from Phengodini. In the absence of a broad phylogenetic analysis it is hard to determine whether 12-articled antennae and telescope-like abdominal segments are synapomorphies of Rhagophthalminae or a Phengodidae + Rhagophthalminae clade. The 12-articled antennae of Rhagophthalminae differ from those of Phengodidae in that the third antennomere is never shorter than the preceding article (i.e., pedicel). The male antennae of Rhagophthalminae are either bipectinate or somewhat serrate, with small sensory appendages on the outer upper edges of one to several flagellar articles (see Ohba et al.,

1996; Kawashima 2000; Kawashima and Satô, 2001; Kawashima and Sugaya, 2003). *Oculogryphus* does not have any of these derived characters and is, therefore, unlikely to be allied to Rhagophthalminae.

Luciolineae are the largest lampyrid subfamily with more than 300 species restricted to the Old World. Males of Luciolineae exclusively possess six abdominal ventrites in males and seven in females (McDermott, 1964; Ballantyne, 1968, 1987a, 1987b; Ballantyne and McLean, 1970; Ballantyne and Lambkin, 2001). The visible sternites are of the second to seventh segments in males. Sternite 8 is membranous and back-folded into the abdominal cavity (Jeng et al., 2003a). The aedeagal sheath, composed of S9 and T9 + 10, is also embedded within the abdomen. The other subfamilies have either seven or eight abdominal ventrites in males. The additional ventrites are exposed segments 8 and 9. The state of six ventrites is derived in Lampyridae and appears to be a good synapomorphy of Luciolineae (Branham and Wenzel, 2001; Ballantyne and Lambkin, 2006). Only two doubtful exceptions—the lampyrid genus *Pristolycus* and an undescribed genus—were found to have six-ventrite abdomens in males among the other lampyrids. Those two genera have well-developed, compressed, and serrate antennae, small eyes, and either lack or have vestigial photic organs in males. These characters make them look quite deviated from typical lucioline genera. However, a molecular phylogenetic study of mitochondrial 16S rDNA sequences supports a close relationship of *Pristolycus* with some Luciolineae groups (Suzuki, 1997). Their true systematic placements need further investigation (Jeng et al., 2002). *Oculogryphus* has eight abdominal ventrites. This is an ancestral state in relation to the six-ventrite abdomen and, as such, this character does not provide evidence for affinity with Luciolineae. *Oculogryphus* may have a basal position relative to typical Luciolineae, or represent a surviving stem group (i.e., a phylogenetic “bridge”) from the latter to the other subfamilies.

Both sexes of adult Luciolineae have well-developed photogenic organs and are able to glow or flash. With few exceptions, the lantern on S6 occupies the entire sternite in both sexes,



fully or partially so on S7 in males and absent in females (Ballantyne, 1968, 1987b; Jeng et al., 1998b). In contrast, genera of Ototretinae are not thus far known to have well-developed lanterns in males. If lanterns are present, they are no more than a pair of vestigial lanterns held over from the larval stage. In anatomy, a lantern is usually accompanied with transparent cuticle ventrally or dorsally. A reduced lantern still keeps the transparent cuticle but in a smaller area in relation to a well-developed lantern. There is no vestige of lanterns in *Oculogryphus* and we did not find any transparent cuticular area on the last few sternites when they were removed from the abdomen and soaked in a solution of potassium hydroxide. This leads us to infer that it is likely to be a plesiomorphic absence. It appears that there is no clear phylogenetic information provided by this character with respect to the placement of *Oculogryphus*.

Compound eyes with emarginate posterior margins occur in several genera of Rhagophthalminae, Phengodidae, and Lampyridae. They are most remarkable in the rhagophthalmid genus *Diophtoma* Pascoe whose compound eyes are almost divided into upper and lower parts by a groove for each. Other genera like *Rhagophthalmus* Olivier, *Ochotyra* Pascoe, *Menghuoius* Kawashima and Satô of Rhagophthalminae and *Nephromma* Wittmer of Phengodidae also have compound eyes that are deeply emarginate. However, simple and slightly emarginate compound eyes also appear in Rhagophthalminae, showing a multistate transformation series across the lineage. In lampyrids, emarginate compound eyes can be found in *Lamprigera* Motschulsky and in Luciolinae like *Lampyroidea* Costa, *Bourgeoisia* Olivier, and *Luciola cowleyi* Blackburn. When present, this character is always associated with greatly enlarged compound eyes that are approximate or nearly contiguous ventrally, but the reverse association is not true. The emarginate eye could be a functional adaptation for some big-eyed cantharoids and may have evolved independently among different lineages. Unfortunately, the compound eye morphology contributes little to our understanding of the phylogenetic placement of the new genus as a result of this diversity.

In regard to Ototretinae, the subfamily is another controversial taxon in Elateroidea.

McDermott (1964) split *Ototreta* Olivier from Luciolinae and added some American genera to form the subfamily, mentioning that the subfamily resembled Drilidae in general appearance. For an unknown reason he placed the subfamily as a tribe of Luciolinae (McDermott, 1966). Crowson (1972) placed Ototretinae in Lampyridae and expanded the definition of the subfamily to incorporate several genera transferred from Drilidae. This was followed by many subsequent authors (e.g., Wittmer, 1979; Nakane, 1991; Lawrence and Newton, 1995; Lawrence et al., 1999; Kawashima et al., 2003, 2005; Ohba, 2004). However, Suzuki's (1997) and Branham and Wenzel's (2001, 2003) phylogenetic analyses all suggested the subfamily was paraphyletic or polyphyletic. Accordingly, Branham and Wenzel (2001) considered Ototretinae of uncertain status within Elateroidea.

It is not our intention to analyze the validity or position of Ototretinae in this paper. However, there are some morphological traits occurring in the subfamily worthy of discussion. In particular, the structure of the abdominal sternites, like the development of the second sternite and location of spiracles, are worthy of discussion in the context of *Oculogryphus*. As suggested by the key above, the Ototretinae can be divided into two major subgroups by the development of S2. The typical subgroup (SG1), including *Drilaster*, *Picodrilus*, *Flabellotreta*, *Mimophaeopterus*, *Ceylanidrilus*, *Gorhamia*, *Lamellipalodes*, *Lamellipalpus*, North American *Brachylampis* Van Dyke, and some others, has S2 short and weakly sclerotized centrally, and is largely concealed by the metatrochanters except the lateral portions in males. In most cases the posterior margin of S2 does not reach the base of the metatrochanters. SG1 genera are usually compact in body shape and have a drilidlike appearance. The other subgroup (SG2), composed of *Stenocladus*, *Harmatelia*, *Falsophaeopterus* and so on, has a long and well developed S2 whose posterior margin reaches the base of the metatrochanters in males. Genera of SG2 are usually elongate in body shape, and less drilidlike than SG1. In addition, SG1 has their abdominal spiracles entirely enclosed by dorsally folded portions of the sternites, a feature easily seen when the



elytra and hind wings are removed. The abdominal spiracles of SG2 are situated at the edge of the pleural membrane and dorsally folded portion of the sternites. Crowson (1972) did not notice these significant differences and lumped all of these genera together when he revived the subfamilial status of Ototretinae and redefined them. That is perhaps why he considered the definition of Ototretinae unsatisfactory and the subfamily to be heterogeneous. We compared the hind-wing venation of *O. fulvus* with several *Stenocladius* and *Drilaster* species, and found it matches well with those of *Stenocladius* but not of *Drilaster*. In addition, the male genitalia of *O. fulvus* resemble those of *Stenocladius* in which the parameres are fused dorsally at the base forming a V-shaped structure (cf. Kawashima, 1999). In contrast, male genitalia of *Drilaster* are considerably abbreviated and have a very different morphology (cf. Kawashima et al., 2005). *Oculogryphus* definitely resembles SG2 more than SG1 in overall morphology. Because the characters differentiating SG1 and SG2 are generally plesiomorphic for cantharoid beetles, it is possible that one of them is defined solely by symplesiomorphies or homoplasies thereby creating a paraphyletic or polyphyletic group. Branham and Wenzel's (2001) phylogenetic tree suggests neither of these groups is monophyletic, but the characters mentioned above were not included in their study.

Another character of *Oculogryphus* worthy of mention is the absence or obscurity of the mesopleuroventral suture. Crowson's (1972) key distinguished Ototretinae from nuclear lampyrid subfamilies (Amydetinae, Luciolinae, Lampyrinae, and Photurinae) partially by the possession of the pleuroventral suture of the mesothorax. After examination of a broad spectrum of genera of the latter four subfamilies, we noticed that the obsolescence of the suture is diverse across them. The well-defined suture is assumed plesiomorphic to cantharoid beetles and simultaneously preserved in several genera of Amydetinae, Lampyrinae, and Photurinae, like *Amydetes* Hoffmannsegg, *Pyrocoelia*, and *Pyrogaster* Motschulsky among others, as well as the other subfamilies. It is not a good diagnostic character for Ototretinae.

In summary, the new genus lacks the major synapomorphic features of Rhagophthalminae and Luciolinae and most of their similarities are likely plesiomorphic. The morphology of *Oculogryphus* also deviates from all other subfamilies except the problematic Ototretinae, which are heterogeneously assembled and essentially defined by presumed symplesiomorphies. The large compound eyes and head make *Oculogryphus* look very different from ototretine genera and instead resembles Luciolinae; it otherwise largely matches the general morphology of Ototretinae (i.e., possessing considerable plesiomorphic characters in relation to those of Lampyridae sensu stricto). This explains why *Oculogryphus* is arguably attributed to Rhagophthalminae, Luciolinae, and Ototretinae simultaneously by McDermott's and Crowson's keys. While *Oculogryphus* is likely a basal lineage of Luciolinae, or a transitional form between Luciolinae and basal groups of Lampyridae, or an allied or true member of the SG2 (nontypical subgroup) of Ototretinae, such an assignment remains far from definitive. Based on Branham and Wenzel's tree, the genus may fall outside of Lampyridae if it is actually closely related to Ototretinae. Herein we temporarily place the new genus in Lampyridae (sensu Crowson) until a clear phylogenetic position is revealed. The genus will hold phylogenetic and evolutionary significance because it may be one of the most basal groups using photic cues for the purposes of mating in lampyrid or cantharoid beetles (assuming that females possess some form of photogenic organs). *Oculogryphus* will be included in a comprehensive phylogenetic analysis of Lampyridae being completed by the senior author. It is greatly hoped that those analyses will illuminate the placement of this enigmatic genus among the fireflies.

#### ACKNOWLEDGMENTS

We are grateful to the late Dr. M. Satô (A.C. 1937–2006) who provided us with the precious material discussed herein; and to Dr. M.A. Branham (University of Florida) and Dr. L.A. Ballantyne (Charles Stuart University, Australia) for comments that improved

the manuscript. We would like to thank Mary Knight, of the AMNH, for her care in seeing this manuscript through production and her skillful assistance with the final figures. This study was supported financially by the National Science Council, Republic of China, grant NSC94-2621-B002-008 and by U.S. National Science Foundation grant DEB-0542909. This is contribution No. 3483 of the Division of Entomology, University of Kansas Natural History of Museum.

# REFERENCES

- Annandale, N. 1900. Observations on the habits and natural surroundings of insects made during the "Skeat Expedition" to the Malay Peninsula, 1899–1900. VI. Insect luminosity: an aquatic lampyrid larva. *Proceedings of the Zoological Society of London* 6: 862–865.
- Annandale, N. 1906. Notes on the freshwater fauna of India. No. III. An Indian aquatic cockroach and beetle larva. *Journal and Proceedings of the Asiatic Society of Bengal (new series)* 2: 105–108.
- Ballantyne, L.A. 1968. Revisional studies of Australian and Indomalayan Luciolini (Coleoptera: Lampyridae: Luciolinae). *University of Queensland Papers Department of Entomology* 2(6): 103–134.
- Ballantyne, L.A. 1987a. Further revisional studies on the firefly genus *Pteroptyx* Olivier (Coleoptera: Lampyridae: Luciolinae: Luciolini). *Transactions of the American Entomological Society* 113(3): 117–170.
- Ballantyne, L.A. 1987b. Luciolinae morphology, taxonomy and behaviour: a reappraisal (Coleoptera, Lampyridae). *Transactions of the American Entomological Society* 113(3): 171–188.
- Ballantyne, L.A., and E. Buck. 1979. Taxonomy and behavior of *Luciola* (*Luciola*) *aphrogeneia*, a new surf firefly from Papua New Guinea. *Transactions of the American Entomological Society* 105(2): 117–137.
- Ballantyne, L.A., and C. Lambkin. 2001. Lampyridae of Australia (Coleoptera: Lampyridae: Luciolinae: Luciolini). *Memoirs of the Queensland Museum* 46(1): 15–93.
- Ballantyne, L.A., and C. Lambkin. 2006. A phylogenetic reassessment of the rare S.E. Asian firefly genus *Pygoluciola* Wittmer (Coleoptera: Lampyridae: Luciolinae). *Raffles Bulletin of Zoology* 54(1): 21–48.
- Ballantyne, L.A., and M.R. McLean. 1970. Revisional studies on the firefly genus *Pteroptyx* Olivier (Coleoptera: Lampyridae: Luciolinae: Luciolini). *Transactions of the American Entomological Society* 96(3): 223–305.
- Blair, K.G. 1927. An aquatic lampyrid larva from S. Celebes. *Transactions of the Entomological Society of London* 1927: 43–45.
- Branham, M.A., and J.W. Wenzel. 2001. The evolution of bioluminescence in cantharoids (Coleoptera: Elateroidea). *Florida Entomologist* 84(4): 565–586.
- Branham, M.A., and J.W. Wenzel. 2003. The origin of photic behavior and the evolution of sexual communication in fireflies (Coleoptera: Lampyridae). *Cladistics* 19(1): 1–22.
- Buck, J.B., and E.M. Buck. 1966. Biology of synchronous flashing of fireflies. *Nature* 211: 562–564.
- Buck, J.B., and E.M. Buck. 1968. Mechanism of rhythmic synchronous flashing of fireflies. *Science* 159: 1319–1327.
- Buck, J.B., and E.M. Buck. 1976. Synchronous fireflies. *Scientific American* 234: 74–85.
- Buschman, L.L. 1984. Biology of the firefly *Pyroactomena lucifera* (Coleoptera: Lampyridae). *Florida Entomologist* 67(4): 529–542.
- Chen, T.-R. 1999. Ecological guide to fireflies of Taiwan. Taipei City: Field Image Press, 189 pp. [In Chinese]
- Chen, T.-R. 2003. Fireflies of Taiwan. Taipei City: Field Image Press, 255 pp. [In Chinese]
- Crowson, R.A. 1955. The natural classification of the families of Coleoptera. London: Nathaniel Lloyd, 187 pp.
- Crowson, R.A. 1972. A review of the classification of Cantharoidea (Coleoptera), with the definition of two new families, Cneoglossidae and Omethidae. *Revista Universidad Madrid* 21(82): 35–77.
- Crowson, R.A. 1981. The biology of the Coleoptera. London: Academic Press, xii + 802 pp.
- DuPorte, E.M. 1960. Evolution of cranial suture in adult Coleoptera. *Canadian Journal of Zoology* 38(4): 655–675.
- Faust, L.F. 2004. Fireflies as a catalyst for science education. *Integrative and Comparative Biology* 44(3): 264–265.
- Fu, X.-H., N. Ohba, F.V. Vencl, and C.-L. Lei. 2005a. Structure, behavior and the life cycle of an aquatic firefly, *Luciola substriata*, in China. *Canadian Entomologist* 137: 83–90.
- Fu, X.-H., N. Ohba, Y.-Y. Wang, and C.-L. Lei. 2005b. Bioluminescent courtship behavior of aquatic firefly *Luciola substriata* (Gorh.)

- (Coleoptera: Lampyridae) in China. *Acta Entomologica Sinica* 48(2): 227–231.
- Furuta, T. 1991. A report of activities for restoration of firefly environment in the educational program in a middle school. In *Association of Natural Restoration of Japan* (editorial commission), The reconstruction of firefly environments. Reconquista, Special No. 1: 95–101. Tokyo: Saiteku, 136 pp. [In Japanese, English summary]
- Green, J.W. 1948. Two new species of Lampyridae from southern Florida, with a generic revision of the Nearctic fauna (Coleoptera). *Transactions of the American Entomological Society* 74: 61–73.
- Green, J.W. 1959. Revision of the species of *Microphotus* with an emendation of the Lampyrini (Lampyridae). *Coleopterist's Bulletin* 13(3): 80–96.
- Grimaldi, D., and M.S. Engel. 2005. *Evolution of the insects*. Cambridge: Cambridge University Press, xv + 755 pp.
- Harvey, E.N. 1957. History of luminescence from the earliest times until 1900. *American Philosophical Society Memoirs* 44: 1–768.
- Ho, J.-Z. 1997. Two firefly species with aquatic larvae in Taiwan. *Natural Conservation Quarterly* 17: 42–46. [In Chinese]
- Ho, J.-Z., and J.-S. Chu. 2002. Map for firefly watching in Taiwan. Taichung City: Morning Star Publisher, 325 pp. [In Chinese]
- Ho, J.-Z., and R.-F. Jong. 1997. *Pristolytus kanoi* in crisis: morphology and behavior. *Natural Conservation Quarterly* 18: 26–31. [In Chinese]
- Imms, A.D. 1933. Scientific results of the Cambridge expedition to the east African Lakes, 1930–1–10. On some aquatic Coleopterous larvae. *Linnean Society's Journal-Zoology* 38: 301–307.
- Jeng, M.-L., M.A. Branham, and P.-S. Yang. 2006b. Revision of the Neotropical genus *Roleta* (Coleoptera: Lampyridae). *Insect Systematics and Evolution* 37(2): 227–239.
- Jeng, M.-L., T.-R. Chen, and P.-S. Yang. 2005. *Luciola anceyi* (Coleoptera: Lampyridae), a firefly capable of all-day mate-finding. *Formosan Entomologist* 25(3): 131–137. [In Chinese, English abstract]
- Jeng, M.-L., J. Lai, and P.-S. Yang. 2003b. Lampyridae: A review of aquatic fireflies with description of a new species. In M.A. Jäch and L. Ji (editors), *Water beetles of China* [Vol. III]: 539–562. Vienna: Zoologische-Botanische Gesellschaft, vi + 572 pp.
- Jeng, M.-L., J. Lai, P.-S. Yang, and M. Satô. 1999. On the validity of the generic name *Pyrocoelia* Gorham (Coleoptera, Lampyridae, Lampyrinae), with a review of Taiwanese species. *Japanese Journal of Systematic Entomology* 5(2): 347–362.
- Jeng, M.-L., P.-S. Yang, and J. Lai. 2003a. Notes on the genus *Luciola* (Coleoptera: Lampyridae, Luciolinae) of Taiwan. *Special Bulletin of the Japanese Society of Coleopterology* 6: 247–262.
- Jeng, M.-L., P.-S. Yang, and M. Satô. 1998a. The genus *Cyphonocerus* (Coleoptera, Lampyridae) from Taiwan and Japan, with notes on the subfamily Cyphonocerinae. *Elytra* 26(2): 379–398.
- Jeng, M.-L., P.-S. Yang, and M. Satô. 2002. Notes on the morphology and systematics of the genus *Pristolytus* Gorham (Coleoptera: Lampyridae). *Japanese Journal of Systematic Entomology* 8(2): 87–108.
- Jeng, M.-L., P.-S. Yang, and M. Satô. 2006a. Synopsis of *Cyphonocerus* (Coleoptera: Lampyridae) with description of new species and key to the genus. *Zoological Studies* 45(2): 157–167.
- Jeng, M.-L., P.-S. Yang, M. Satô, J. Lai, and J.-C. Chang. 1998b. The genus *Curtos* (Coleoptera, Lampyridae, Luciolinae) of Taiwan and Japan. *Japanese Journal of Systematic Entomology* 4(2): 331–347.
- Kamei, I. 1989. One trial for firefly's recovery and its conservation in Yokosuka. *Nature and Insects* 24(8): 13–18. [In Japanese]
- Kanda, S. 1935. *Hotaru*. Tokyo: Association of Bioluminescence Research of Japan, 496 pp. [In Japanese]
- Kawashima, I. 1999. The lampyrid beetles of the genus *Stenocladus* (Coleoptera, Lampyridae) of the Ryukyu Islands, Southwest Japan, with descriptions of two new species. *Elytra* 27(1): 141–158.
- Kawashima, I. 2000. A redescription of *Rhagophthalmus ingens* Fairmaire (Coleoptera, Rhagophthalmidae) from northern Vietnam, with establishment of a new genus in the family. *Elytra* 28(1): 131–140.
- Kawashima, I., and M. Satô. 2001. Three new species of the genus *Rhagophthalmus* (Coleoptera, Rhagophthalmidae) from southeast Asia. *Elytra* 29(2): 423–434.
- Kawashima, I., and H. Sugaya. 2003. An additional new species of the genus *Rhagophthalmus* (Coleoptera, Rhagophthalmidae) from Taiwan, with a key to the males of the Taiwanese and Japanese species. *Elytra* 31(2): 353–359.
- Kawashima, I., H. Suzuki, and M. Satô. 2003. A check-list of Japanese fireflies (Coleoptera, Lampyridae and Rhagophthalmidae). *Japanese Journal of Systematic Entomology* 9(2): 241–261.
- Kawashima, I., F. Satou, and M. Satô. 2005. The lampyrid genus *Drilaster* (Coleoptera,

- Lampyridae, Otoretinae) of the Ryukyu Archipelago, Southwest Japan. *Japanese Journal of Systematic Entomology* 11(2): 225–262.
- Kazantsev, S.V. 2006. New firefly taxa from Hispaniola and Puerto Rico (Coleoptera: Lampyridae), with notes on biogeography. *Russian Entomological Journal* 15(4): 367–392.
- Kobayashi, H. 1991. A report of restoration of natural environment for firefly from Shiojiri City. In *Association of Natural Restoration of Japan* (editorial commission), *The reconstruction of firefly environments. Reconquista, Special No. 1*: 65–73. Tokyo: Saiteku, 136 pp. [In Japanese, English summary]
- Konishi, M. 1997. Fireflies in Japanese literature. *Insectarium* 34(5): 34–39. [In Japanese]
- Kukalová-Peck, J., and J.F. Lawrence. 1993. Evolution of the hind wing in Coleoptera. *Canadian Entomologist* 125(2): 181–258.
- Lawrence, J.F., and E.B. Britton. 1994. *Australian beetles*. Carlton: Melbourne University Press, x + 192 pp.
- Lawrence, J.F., and A.F. Newton, Jr. 1995. Families and subfamilies of Coleoptera (with selected genera, notes, references and data on family-group names). In J. Pakaluk and S. A. Slipinski (editors), *Biology, phylogeny, and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson* [Vol. 2]: 779–1092. Warszawa: Muzeum i Instytut Zoologii PAN, vi + 560–1092 pp.
- Lawrence, J.F., A.M. Hastings, M.J. Dallwitz, T.A. Paine, and E.J. Zurcher. 1999. *Elateriformia* (Coleoptera): descriptions, illustrations, identification, and information retrieval for families and subfamilies: Lampyridae [version of 9 October 2005]. <http://delta-intkey.com/elateria/www/lamp.htm>. [website valid as of September 10, 2007]
- Lloyd, J.E. 1971. Bioluminescent communication in insects. *Annual Review of Entomology* 16: 97–122.
- Lloyd, J.E. 1973. Models for the mating protocol of synchronously flashing fireflies. *Nature* 245: 268–270.
- Lloyd, J.E. 1979. Sexual selection in luminescent beetles. In M.S. Blum and N.B. Blum (editors), *Sexual selection and reproductive competition in insects*, 293–342. New York: Academic Press, xi + 463 pp.
- Lloyd, J.E. 1997. On research and entomological education, and a different light in the lives of fireflies (Coleoptera: Lampyridae: *Pyroctomena*). *Florida Entomologist* 80(2): 120–131.
- Lloyd, J.E. 1998. On research and entomological education. II. A conditional mating strategy and resource-sustained lek (?) in a classroom firefly (Coleoptera: Lampyridae, *Photinus*). *Florida Entomologist* 81(3): 261–272.
- Lloyd, J.E. 1999. On research and entomological education. III. Firefly brachyptera and wing “polymorphism” at pitkin marsh and watery retreats near summer camps (Coleoptera: Lampyridae: *Pyroptoga*). *Florida Entomologist* 82(2): 165–179.
- Lloyd, J.E. 2000. On research and entomological education. IV. Quantifying mate search in a perfect insect-seeking true facts and insight (Coleoptera: Lampyridae, *Photinus*). *Florida Entomologist* 83(3): 211–218.
- Lloyd, J.E. 2001. On research and entomological education. V. A species concept for fireflies, at the bench and in old fields, and back to the Wisconsin glacier. *Florida Entomologist* 84(4): 587–601.
- Lloyd, J.E. 2002. Lampyridae Latreille 1817. In R.H. Arnett, Jr., M.C. Thomas, P.E. Skelley and H. Frank (editors), *American beetles* [Vol. 2]: 187–196. Boca Raton, FL: CRC Press, xiv + 861 pp.
- Lloyd, J.E. 2003. On research and entomological education. VI. Firefly species and lists, old and now. *Florida Entomologist* 86(2): 99–113.
- Lloyd, J.E., S.R. Wing, and T. Hongtrakul. 1989. Flash behavior and ecology of Thai *Luciola* fireflies (Coleoptera: Lampyridae). *Florida Entomologist* 72(1): 80–85.
- Maulik, S. 1921. New Indian drilid beetles. *Proceedings of the Zoological Society of London* 1921: 579–586.
- Mayor, A. 2000. The first fossil hunters: paleontology in Greek and Roman times. Princeton, NJ: Princeton University Press, xx + 361 pp.
- McDermott, F.A. 1964. The taxonomy of the Lampyridae (Coleoptera). *Transactions of the American Entomological Society* 90: 1–72.
- McDermott, F.A. 1966. Lampyridae. In W.O. Steel (editor), *Coleopterorum catalogus supplementa, pars 9* (editio secunda): 1–149. S-Gravenhage: W. Junk, 149 pp.
- Murakami, M. 1991. A history of firefly preservation activities in Japan. In *The Association of Natural Restoration of Japan* (editorial commission), *The reconstruction of firefly environments. Reconquista, Special No. 1*: 23–32. Tokyo: Saiteku, 136 pp. [In Japanese, English summary]
- Nakane, T. 1991. Lampyrid insects of the world. In *The Association of Natural Restoration of Japan* (editorial commission), *The Reconstruction of Firefly Environments. Reconquista*,

- Special No. 1: 3–11. Tokyo: Saiteku, 136 pp. [In Japanese, with English summary]
- Nallakumar, K. 2003. Synchronously flashing aggregative fireflies of peninsular Malaysia. *Biodiversity* 4(2): 11–16.
- Ohba, N. 1983. Studies on the communication system of Japanese fireflies. Science Report of the Yokosuka City Museum 30: 1–62.
- Ohba, N. 2004. Mystery of fireflies. Yokosuka: Yokosuka City Museum, 139 pp. [In Japanese]
- Ohba, N., and Y. Goto. 1991. Morphology and behavior of the firefly, *Pristolycus sanguratus* (Coleoptera: Lampyridae). Science Report of the Yokosuka City Museum 39: 1–5. [In Japanese, English summary]
- Ohba, Y., and P.-S. Yang. 2003. Flash patterns and communication system of the Taiwan firefly, *Luciola cerata* Olivier. Science Report of the Yokosuka City Museum 50: 1–12. [In Japanese, English summary]
- Ohba, N., Y. Goto, and I. Kawashima. 1996. External morphology and behavior of *Rhagophthalmus ohbai* Wittmer, 1994 (Coleoptera; Rhagophthalmidae) and its habitat. Science Report of the Yokosuka City Museum 44: 1–19. [In Japanese]
- Olivier, E. 1907. Coleoptera. Fam. Lampyridae. In P. Wytsman (editor), *Genera Insectorum*, Fasc. 53: 1–74 Brussels: Verteneuil and Desmet, 74 pp. + 5 pls.
- Olivier, E. 1910. Lampyridae. In S. Schenkling (editor), *Coleopterorum catalogus*, Pars. 9: 1–68. Berlin: W. Junk, 68 pp.
- Othman, J., and R. Othman. 1998. Economic benefits from wetland biodiversity: case of firefly recreation in Malaysia. *Tropical Biodiversity* 5: 65–74.
- Sivinski, J.M., J.E. Lloyd, S.L. Beshers, D.R. Lloyd, R.G. Sivinski, R.T. Sullivan, and E. Peterson. 1998. A natural history of *Pleotomodes needhami* Green (Coleoptera: Lampyridae): a firefly symbiont of ants. *Coleopterist's Bulletin* 52(1): 23–30.
- Suzuki, H. 1997. Molecular phylogenetic studies of Japanese fireflies and their mating systems (Coleoptera: Cantharoidea). Tokyo Metropolitan University Bulletin of Natural History 3(1): 1–53.
- Trimmer, B.A., J.R. Aprille, D.M. Dudzinski, C.J. Lagace, S.M. Lewis, T. Michel, S. Qazi, and R.M. Zayas. 2001. Nitric oxide and the control of firefly flashing. *Science* 292(5526): 2486–2488.
- Wittmer, W. 1937. Beitrag zur Kenntnis der indomalayischen Malacodermata (Coleoptera). Mitteilungen der Schweizerischen Entomologischen Gesellschaft 17: 209–210.
- Wittmer, W. 1979. Zur Kenntnis der Lampyridae der orientalischen Region (Coleoptera). Entomologische Arbeiten aus dem Museum G. Frey Tutzing bei München 28: 83–92.
- Wu, C.-F. [= Hu, J.]. 1937. Family Lampyridae. In C.-F. Wu (editor), *Catalogus insectorum sinensium* [Vol. III]: 377–385. Peiping [=Beijing]: Fan Memorial Institute of Biology.
- Yamamoto, T. 1968. Fireflies. The Nature and Insects 3(6): 18–20. [In Japanese]
- Yang, P.-S. 1998. Fireflies. Taipei City: Society of Wild and Nature Conservation, 82 pp. [In Chinese]

Complete lists of all issues of the *Novitates* and the *Bulletin* are available at World Wide Web site <http://library.amnh.org/pubs>. Inquire about ordering printed copies via e-mail from [scipubs@amnh.org](mailto:scipubs@amnh.org) or via standard mail from: American Museum of Natural History, Library—Scientific Publications, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009.